

# LIFE HISTORY STUDIES ON THE RED SEA SOFT CORAL *XENIA MACROSPICULATA* GOHAR, 1940. II. PLANULAE SHEDDING AND POST LARVAL DEVELOPMENT

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## ABSTRACT

Sexual reproduction of the soft coral *Xenia macrospiculata* Gohar, 1940 was studied for a four year period at the Gulf of Eilat (Red Sea). Ripe eggs detach successively from the mesenteries into the polyp cavities, where fertilization probably occurs. Subsequently, they pass to special brooding pouches situated near the anthocodial bases. Embryogenesis takes place in these endodermal chambers and after maturation planulae are shed via temporary openings found among the polyps. The planulation period lasts for 4–5 months (May–September) every year. Larval expulsion occurs at night in bi-weekly cycles during interlunar phases: near the first and the last moon quarters. Colony fecundity depends on its size: large colonies are estimated to produce several hundred larvae per polyp each year. Although little information exists on other planulating octocorals, the study indicates that *X. macrospiculata* exhibits a remarkably high reproductive potential, which contributes to its dominance in the Red Sea coral reefs.

Planulae of *X. macrospiculata* share common morphological features with other octocorals. The only movement exhibited by them is slow crawling over the substrate. They possess a very short planktonic phase and metamorphose into polyps immediately after settlement. These traits enable efficient colonization of available reef surfaces and hence, development of dense populations.

## INTRODUCTION

Studies on the life history of Octocorallia indicate that a variety of reproductive patterns are adopted by different species (Suzuki, 1971; Goldberg and Hamilton, 1974; Grigg, 1977; Hartnoll, 1975, 1977; Weinberg and Weinberg, 1979; Yamazato and Sato, 1981; Benayahu and Loya, 1983). For a long period soft corals (order Alcyonacea) were considered to be oviparous (Hickson, 1901; Matthews, 1917). This generality was based on the study of very few species, and mainly on *Alcyonium digitatum* (Linnaeus, 1758). The early surveys concerning the xeniid soft corals did not present any information about their mode of sexual reproduction (Bourne, 1895; Ashworth, 1899, 1900; Hickson, 1931). The studies of Gohar (1940a, b) and Gohar and Roushdy (1961) pointed out for the first time that xeniids reproduce by planulae shedding. These publications concentrate on the natural history of *Heteroxenia fuscescens* (Ehrenberg, 1834) and its reproduction. In addition, Gohar (1940a) stated that *Xenia macrospiculata* reproduces by planulation. So far, nothing more is known about the dynamics of the process or development of planulae into polyps. We have

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previously described the annual cycle of gonadal development of *X. macrospiculata* (Benayahu and Loya, 1984).

The present work is based on a 4.5 year study of the abundant Red Sea soft coral *X. macrospiculata* (Benayahu and Loya, 1981). This is the first quantitative account on the dynamics of sexual reproduction of a planulating, reef-dwelling soft coral. It deals with the mode of planular brooding, the annual pattern of larval shedding, the timing of planulation, and its correlation with lunar periodicity. In addition we describe the morphological features of the planulae, their behavior, and the sequence of events leading to the development of a young colony.

## MATERIALS AND METHODS

During the study on the gonadal development of *X. macrospiculata* (March, 1977–September, 1981), monthly samples were examined for planulae within the colonies (for details on study locality and sampling procedure see Benayahu and Loya, 1984). These observations indicated that larvae are found during June–September. In the present survey a quantitative examination was carried out during May–September, 1980, in order to determine the detailed reproductive state of the population throughout the breeding season. During these months the shallow water population (3–5 m) at Muqebela', located 12 km south of Eilat, was sampled 34 times. Each sample contained approximately 20 large colonies collected randomly. The colonies were carefully detached from the substrate, placed separately in plastic bags with sea water, and carried to the Marine Biological Laboratory (M.B.L.) at Eilat. Then each colony was transferred into a 1 liter aerated container, made of transparent plastic. The laboratory light regime simulated natural light conditions. This sampling procedure enabled us to continuously maintain a total number of 750 colonies during May–September, 1980 and to detect planulation at the laboratory. The containers were inspected for larvae every 7–8 hours. After planulae shedding, the colonies were removed to other containers for further observations. The planulae were counted and examined by a stereoscopic binocular microscope. A week after collection the colonies were bisected longitudinally and examined for presence of gonads or planulae (see Benayahu and Loya, 1984 for further details).

## RESULTS

### *The planulation period and spawning*

Xeniid species such as *Heteroxenia fuscescens* and *H. ghardagensis* Gohar, 1940 often tend to expel their larvae shortly after collection from the reef, or under any other stressful conditions (pers. obs.). Such a phenomenon has never been observed among colonies of *X. macrospiculata*, despite the sampling of hundreds of corals throughout the research period. Examination of the monthly samples (Benayahu and Loya, 1984), indicates that females brood their planulae in June–September (Table I). The larvae were found inside special chambers at the upper part of the polyp cavities, near the anthocodial bases (Fig. 1a).

The continuous population sampling during May–September, 1980 indicated that the majority of the colonies bear gonads. Toward September the percent of sexual colonies decreased (Benayahu and Loya, 1984). Examination of sections of living male colonies showed that in addition to the sperm sacs attached to the mesenteries, other spermaries were free in the polyp cavities. Starting in May, the endodermal surroundings of the mature testes ruptured and mature spermatozoa were expelled. Such spermatozoa possess an elongated head, (5–7  $\mu\text{m}$ ), with a pointed anterior, and

TABLE I

*Presence of planulae within brooding pouches of Xenia macrospiculata during 1977–1981*

Year	June	July	August	September
1977	—	+	+	+
1978	+	+	+	—
1979	—	+	+	+
1980	+	+	+	—
1981	+	+	+	—

a tail measuring 45–50  $\mu\text{m}$ . Spawning was recorded within a wide range of testis diameters (100–400  $\mu\text{m}$ ). during the spawning period the polyp cavities also contained many empty sperm sacs, recognizable by their wrinkled surface. Although sperm release was not observed, it is presumed that it took place through the polyp mouth.

The ripe eggs of *X. macrospiculata* detach from the mesenteries into the coelenteron, where they are probably fertilized. Then the eggs pass into special endodermal chambers (Fig. 1a), which we termed brooding pouches because larval embryogenesis occurs there. The color of the surrounding walls of the pouches is dark brown due to the high content of zooxanthellae. Each individual brooding pouch contains 15–30 embryos of the same developmental stage. Examination of colonies during the planulation period revealed that they simultaneously bear oocytes and planulae of various developmental stages.

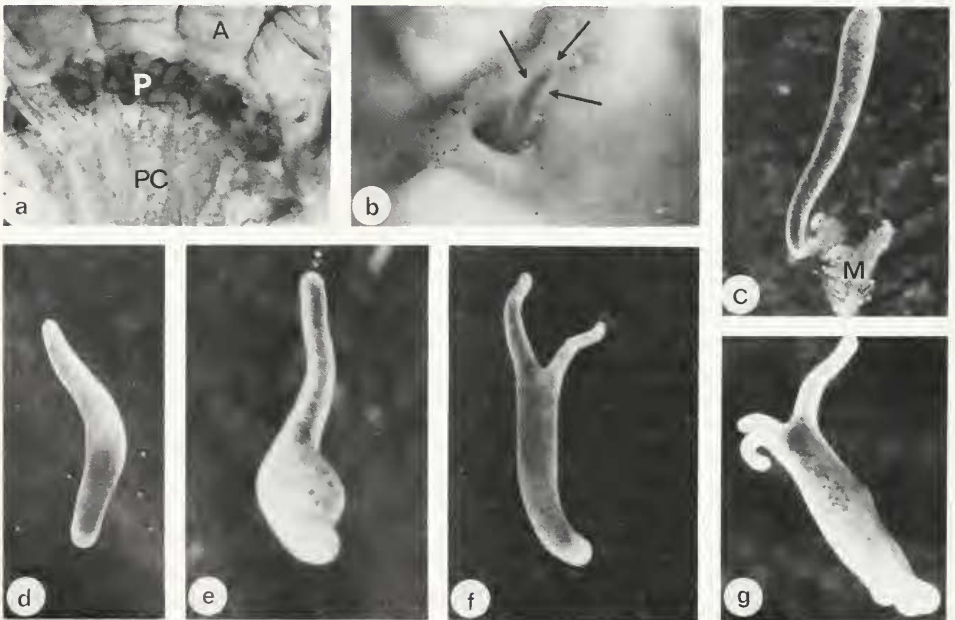


FIGURE 1. Planulae of *Xenia macrospiculata* a: Brooding pouches with young planulae ( $\times 7$ ), anthocodium (A), planulae (P), polyp cavity (PC). b: Planula emission through a temporary opening ( $\times 15$ ), arrows indicate the emerged larva. c: Mature planula attached by mucus (M) to the substrate ( $\times 25$ ). d, e: Contracted planulae ( $\times 25$ ). f, g: Malformations of planulae ( $\times 25$ ).

### Timing of planulae shedding

The close examination of 750 colonies during May–September, 1980 indicates that planulae shedding occurs with a marked periodicity. Figure 2 demonstrates the reproductive state of the population during this period. The upper part of this figure shows the dates when planulation was observed and the percent of female colonies shedding planulae during the study. The lower part of the figure represents the percent of colonies in the samples which contained planulae in their brooding pouches. These results indicate that planulation occurs twice within a lunar cycle: near the first and the last moon quarters. During each lunar quarter, planulation lasts a few days (Fig. 2). The first planulation started on 21 May and the last was observed on 21 August. The presence of some female colonies with planulae embryos at the end of August strongly suggests that the sexual reproduction continued during September. Hence, the annual reproductive period of *X. macrospiculata* lasts for 4–5 months annually (see also Table I).

Planulae shedding occurs at dusk, starting at about 1800 and becoming more intense by 2200. Within a colony this process is very rapid and it takes only a few minutes for thousands of larvae to emerge. The planulae are shed through temporary openings located among the anthocodial bases (Fig. 1b), which close immediately after planulation.

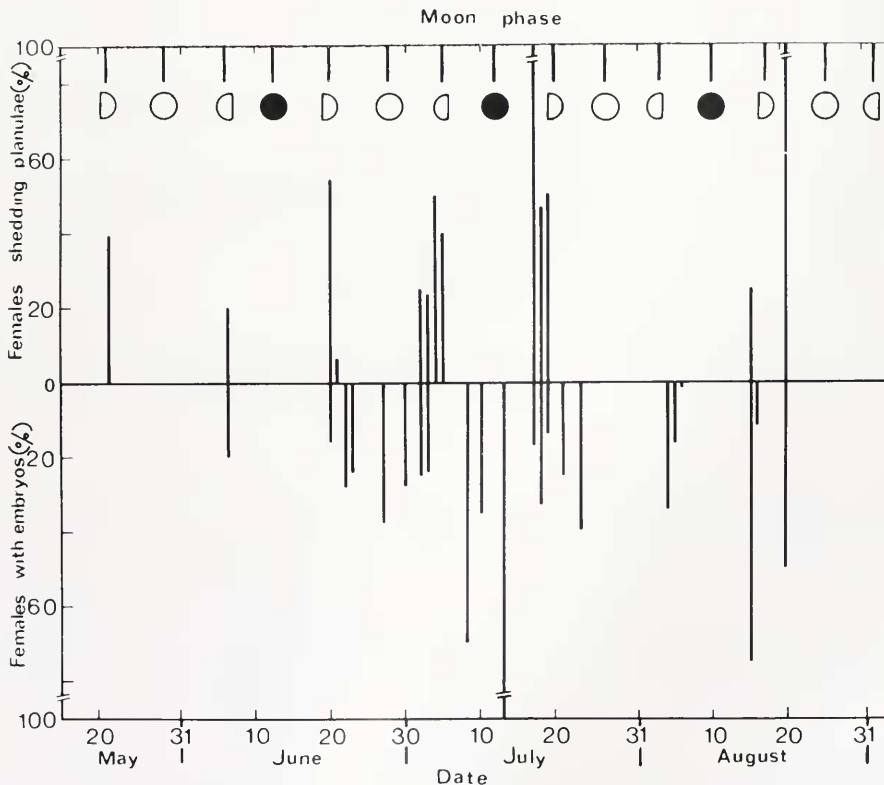


FIGURE 2. Reproductive state of female colonies of *Xenia macrospiculata* during May–August, 1980. The upper scale indicates the moon phase: D—first quarter, O—full moon, Q—last quarter, ●—new moon.



Table II presents the number of planulae emitted by seven large colonies of similar size kept at the M.B.L. The colonies were collected on 15 July and their first planulation was recorded two days later. Planulation started three days before the first lunar quarter and it continued for three successive nights. Note the low number of larvae obtained on the first night (17 July). On 21 July, the colonies were sectioned. No planulae were found in the brooding pouches, but many oocytes were attached to the mesenteries.

Figure 3 presents the number of planulae extruded by the female colonies during May–September, 1980. These results demonstrate that the number of larvae released per colony during one night is highly variable. In addition, 40% of the females did not planulate on the expected date; half of them contained immature larvae within their brooding pouches, while the other half bore only oocytes. These results point out that during the breeding season, a substantial part of the population does not shed every lunar quarter. Note that only 6% of the females released numerous larvae on a given night (several thousand per colony, Fig. 3).

### *Morphology and behavior of planulae*

The planulae of *X. macrospiculata* are slender, reaching 2.5 mm in length and 0.15 mm in width (Fig. 1c). When fully extended they are broad at the oral end, and taper gradually toward the other end. Although their body is ciliated, planulae have never been observed swimming. Their color is cream gray, with brown spots, due to the presence of zooxanthellae. *Xenia* planulae are capable of contraction and hence of changing their body shape (Fig. 1d, e). This behavior also alters the color due to the change in the distribution of zooxanthellae. After shedding, the larvae lie vertically on the bottom of the containers, with their aboral end facing the substrate. Secreted mucus fastens the planulae to the substrate (Fig. 1c). Occasionally, the larvae change their position on the substrate by slow crawling facilitated by ciliary movement and body contractions. A negligible number of abnormal planulae (malformations) were recorded. From thousands of planulae examined only a few were the result of incomplete fusion of two or three eggs (Fig. 1f, g).

### *Development of the primary polyp and a young colony*

Experiments dealing with substrate selection by planulae of *X. macrospiculata* (Benayahu, 1982) supply information on their metamorphosis into polyps. This study

TABLE II

*Number of planulae extruded by seven colonies of Xenia macrospiculata during successive nights in July, 1980*

Colony No.	No. of planulae			
	17 July	18 July	19 July	20–21 July
1	226	thousands	1000	0
2	3	1000	3000	0
3	10	700	350	0
4	182	thousands	60	0
5	14	0	7	0
6	262	700	12	0
7	137	thousands	thousands	0

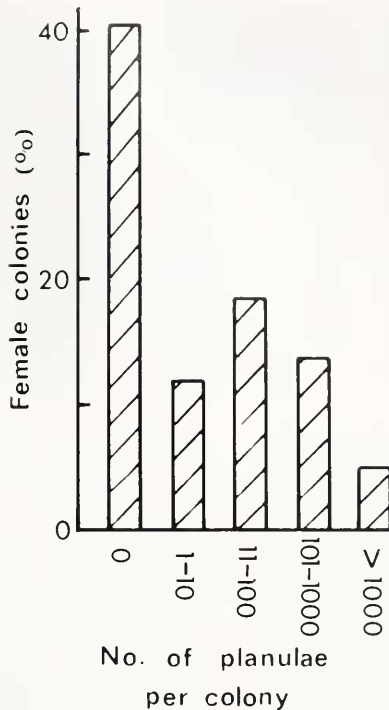


FIGURE 3. Number of planulae extruded by colonies of *Xenia macrospiculata*.

indicates that on the second day after extrusion the larvae become shorter, attaining a pear-like shape. A day later, the attached planulae become rounded, reaching  $\frac{1}{5}$  of their original length. On the 4th day, the aboral side becomes disk-like with 8–10 tentacular grooves at the oral end. On the 5th day each young polyp bears 8 primary tentacles still lacking pinnules. Later development during the 6–7th day causes unequal growth of the tentacles and the polyp body becomes elongated (Fig. 4a). During the next two days the tentacles gradually grow, achieving an even length (Fig. 4b). On the 9th day after larval emission, some tentacles bear the first pair of pinnules (Fig. 4c). Two weeks after shedding, the polyps develop four pairs of pinnules, while another two pairs are formed on the 17–18th day (Fig. 4d). One month old polyp, measures 3–5 mm and has 7–8 pairs of pinnules on each tentacle. Spicules are found at an early stage of development (Fig. 4b, c), sometimes even on the third day after shedding. Their abundance gradually increases, becoming more common on the aboral side of the tentacles.

Field experiments dealing with growth of young colonies of *X. macrospiculata* (Benayahu, 1982) indicate that budding of a second polyp occurs 3–4 months after settlement. At an age of 5–6 months a young colony bears four polyps (Fig. 4e).

#### DISCUSSION

Recent studies on the reproduction of planulating anthozoans are mainly concerned with sea anemones (Chia, 1976; Ottaway, 1979; Jennison, 1981), scleractinian corals (Harrigan, 1972; Stimson, 1976, 1978; Rinkevich and Loya, 1979a, b; Kojis and

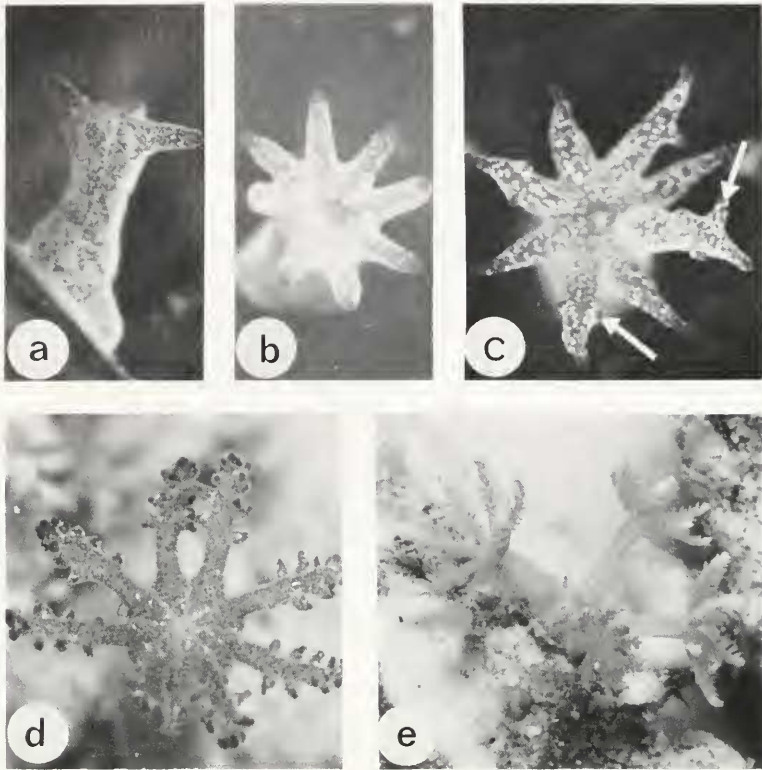


FIGURE 4. Development of a polyp and young colony of *Xenia macrospiculata*. a: 6-7 days old polyp ( $\times 8$ ). b: 8-9 days old polyp with white sclerites ( $\times 7$ ). c: 9-10 days old polyp, arrows indicate first pair of pinnules ( $\times 12$ ). d: 17-18 days old polyp ( $\times 12$ ). e: 5-6 months old colony ( $\times 1.5$ ).

Quinn, 1981a; Moorsel, 1981; Fadlallah and Pearse, 1982, Sammarco, 1982), and gorgonians (Théodor, 1967; Kinzie, 1970; Grigg, 1977; Weinberg and Weinberg, 1979). The information gathered on the different species within each group indicates the adoption of a variety of reproductive patterns (Chia, 1976; Grigg, 1977, Kojis and Quinn, 1981a, b). Although for many years soft corals had been regarded as oviparous species, several of them were reported to reproduce through planulation (Table III). The boreal species *Alcyonium hibernicum* exhibits a parthenogenic mode of larval development (Hartnoll, 1977). The temperate soft coral *A. siderium* planulates each year for a period of one month (Sebens, 1983). The other species presented in Table III are Red Sea xeniids, reported from Gohar's study (1940a). A month-long planulation period of *X. macrospiculata* as reported by Gohar is in direct contrast to the results presented here (Fig. 2). In addition, Gohar did not find synchronization between larval shedding and lunar phase.

Kojis and Quinn (1981b) discuss the difficulties in detecting planulation among stony corals. We further suggest that larval shedding by *X. macrospiculata* exhibits several features that require a comprehensive study. We have shown that colonies of *X. macrospiculata* are dioecious, with no sexual dimorphism, and that sex ratio favors higher abundance of males (Benayahu and Loya, 1984). Further life history features presented in this paper indicate that (1) female colonies may planulate in intervals

TABLE III

*Planulating soft coral species and their reproductive period*

Species	Planulation period
<i>Alcyonium hibernicum</i> (Renouf, 1931)	July
<i>A. siderium</i> Verrill, 1922	August
<i>Anthelia glauca</i> Lamarck, 1816	no direct observation
<i>Heteroxenia fuscescens</i> (Ehrenberg, 1834)	March–September
<i>H. ghadaqensis</i> Gohar, 1940	May–June
<i>Sympodium caeruleum</i> Ehrenberg, 1834	no direct observation
<i>Xenia blumi</i> Schenk, 1896	May–June
<i>X. hicksoni</i> Ashworth, 1899	May–June
<i>X. macrospiculata</i> Gohar, 1940	October
<i>X. umbellata</i> Savigny, 1816	October

of two weeks or more, (2) the number of planulae extruded per colony during a particular night is highly variable, and (3) larval shedding of an individual colony lasts for only a few minutes. Under these circumstances, a long term population study examining large sample sizes is required to follow the detailed pattern of planulation.

Studies on internally brooding stony corals, sea anemones, and gorgonians indicate that planulae development occurs inside the polyp cavities (Rinkevich and Loya, 1979a; Weinberg and Weinberg, 1979; Jennison, 1981). However, among xeniids unique brood pouches function as sites for embryogenesis. We have noticed that during the reproductive season female colonies of *X. macrospiculata* may simultaneously contain oocytes and planulae of various developmental stages. Even though we lack information on the length of the planulation period of an individual colony, the present results indicate that a successive maturation of eggs occurs and that they are transferred into the brooding pouches for further development. The continuous gametogenesis of each colony (Benayahu and Loya, 1984) supports the assertion that several cycles of larval release take place every year.

The number of eggs produced by a *Xenia* colony is determined by the length of its polyp cavity (Benayahu and Loya, 1984). Even assuming that only some of the oocytes in a polyp develop into planulae, it is still probable that several hundred larvae are produced annually by each polyp. Grigg (1977) found that the gorgonian *Muricea californica* produces an average of 1.6 planulae per polyp and *M. fruticosa* 3.8 per polyp. Théodor (1967) reported a similar figure of 3–5 planulae a year for the Mediterranean gorgonian *Eunicella stricta*. The soft coral *Parerythropodium fulvum* produces 18–24 planulae per polyp each year (Benayahu and Loya, 1983). Fecundity of scleractinians is based on the number of planulae or mature eggs extruded by a coral colony at a time (Harrigan, 1972; Rinkevich and Loya, 1979b; Kojis and Quinn, 1981b). However, it is difficult to compare these results with fecundity of octocorals, since the studies on stony corals do not present the total annual planulae production of a polyp (see also Kojis and Quinn, 1981b). Nevertheless, the release of several thousand planulae by an individual colony of *X. macrospiculata* in one night (Fig. 3) indicates a markedly high fecundity. Continuous larval shedding during the reproductive season leads us to suspect that such high levels of larval production are maintained over long periods of time.

The present paper demonstrates some similarities between *X. macrospiculata* and other xeniid species studied by Gohar (1940a). The general mode of their larval development in brooding pouches and larval emission through temporary gonopores



are alike among the Xenidae. Octocoral planulae spend a relatively short period of a few hours in the water column and tend to settle on the substrate very soon after shedding (Gohar, 1940a; Weinberg and Weinberg, 1979). The motility of the planulae of *X. macrospiculata* is limited to a sluggish crawling on the substrate. Their short planktonic phase and the rapid metamorphosis into polyps support their ability to quickly colonize available space. However, these features restrict the distribution of the species and encourage the development of local aggregations of *Xenia* beds (Benayahu and Loya, 1981). In addition, *X. macrospiculata* exhibits a unique movement ability (Benayahu and Loya, 1981) and a rapid mode of asexual reproduction (Benayahu, 1982), which enable the colonies to settle successfully on the reef surface (Benayahu and Loya, in prep.). Other traits of this coral such as small body size, early age of first reproduction, and prolonged period of gametogenesis (Benayahu and Loya, 1984) benefit marked reproductive effort. Further information is needed on the life histories of other alcyonacean species, in order to compare various tactics evolved by these corals. However, the results of this study suggest that *X. macrospiculata* is an opportunistic species with a remarkable reproductive potential, causing its dominance on the Red Sea coral reefs.

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